Preharvest UV-C radiation influences physiological, biochemical, and transcriptional changes in strawberry cv. Camarosa

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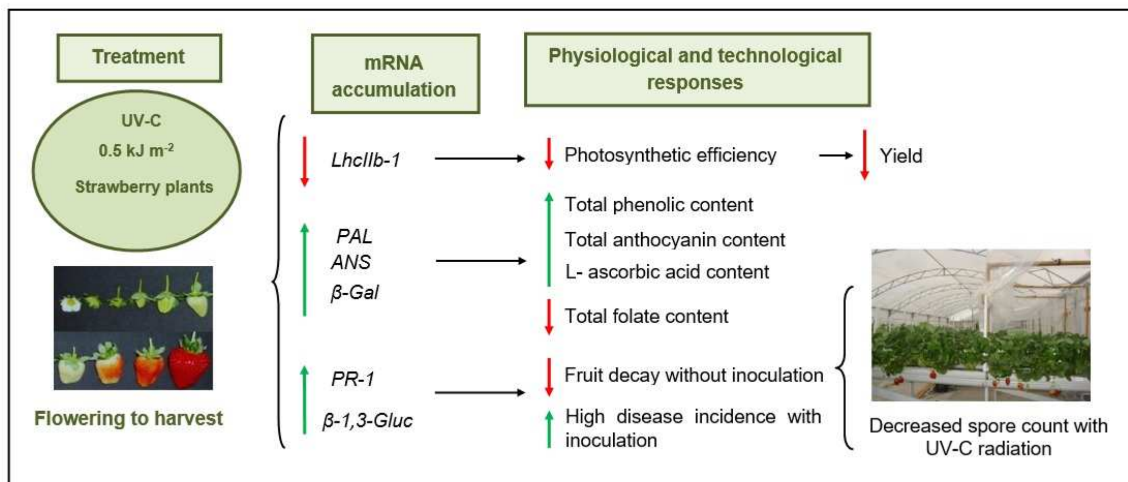
Graphical Abstract



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1 **Preharvest UV-C radiation influences physiological, biochemical, and transcriptional**
2 **changes in strawberry cv. Camarosa**
3

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23 **Abstract**

24 Ultraviolet C (UV-C) radiation is known for preventing fungal decay and enhancing
25 phytochemical content in fruit when applied postharvest. However, limited knowledge is
26 available regarding fruit responses to preharvest application of UV-C radiation. Thus, the
27 effects of UV-C radiation on photosynthetic efficiency, dry matter accumulation and
28 partitioning, fruit yield and decay, phytochemical content, and relative transcript
29 accumulation of genes associated with these metabolic pathways were monitored in
30 strawberry (*Fragaria* x *ananassa* Duch.) cv. Camarosa. A reduction in photosynthetic
31 efficiency was followed by a decrease in light harvesting complex *LhcIIb-1* mRNA
32 accumulation as well as a decrease in yield per plant. Phenylalanine ammonia lyase activity,
33 phenolic, anthocyanin, and L-ascorbic acid contents were higher in UV-C treated fruit. In
34 addition, preharvest UV-C treatment reduced microorganism incidence in the greenhouse and
35 on the fruit surface, increased the accumulation of *β-1,3-Gluc* and *PR*-1 mRNA, and
36 prevented fruit decay.

37

38 **Keywords**: *Fragaria* x *ananassa* Duch.; abiotic stress; antioxidants; gray mold disease.

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39 **1. Introduction**

40 Strawberry (*Fragaria* × *ananassa* Duch.) pseudo fruit, henceforth named fruit, is rich
41 in bioactive compounds, such as L-ascorbic acid, folates, and phenolic compounds including
42 anthocyanins (Giampieri et al., 2015; Tulipani et al., 2011). This fruit is characterized by high
43 respiration and transpiration rates, low mechanical resistance, and high susceptibility to gray
44 mold caused by *Botrytis cinerea* (Neri et al., 2014). In order to control gray mold, seasonal
45 spraying of fungicides is carried out during fruit development, and postharvest fruit are cold
46 stored under modified atmosphere (Barrios et al., 2014; Feliziani et al., 2015). However, the
47 use of fungicides poses significant health risks to consumers, and demand for strawberries
48 produced with fewer fungicides is increasing (Feliziani et al, 2015).

49 Alternative control methods that do not leave residues, such as postharvest UV-C
50 radiation, have been shown to prevent decay and improve fruit quality (Baka et al., 1999;
51 González-Aguilar et al., 2007; Maharaj et al., 1999; Severo et al., 2015a, 2015b). In response
52 to postharvest UV-C, tomato fruit developed biochemical and physical barriers against
53 *Botrytis cinerea* growth by accumulating phenolic compounds, defense proteins, and
54 developing fruit surface modifications (Charles et al., 2008a, 2008b, 2008c). Additionally, it
55 has been reported that postharvest UV-C radiation induces secondary metabolites production
56 that protect fruit against abiotic and biotic stresses (Pombo et al., 2011). Furthermore, these
57 metabolites (phenolic compounds, anthocyanins, carotenoids) also play an important role in
58 fruit quality with impact on human health (Giampieri et al., 2015).

59 On the other hand, few studies have investigated preharvest UV-C application, and the
60 mechanism of action preventing decay and improving fruit quality is not well understood.
61 Tomato fruit on the vine treated with UV-C showed delayed ripening and inhibition of
62 *Penicillium digitatum* growth (Obande et al., 2011). The effects of preharvest UV-C on
63 bioactive compounds content in strawberries appears to be cultivar dependent (Xie et al.,

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64 2015). In addition, excess UV-B and UV-C radiation during growth of *Arabidopsis thaliana*
65 has deleterious effects on plant cells, including DNA damage and oxidation of cellular
66 components with consequent deleterious effects on photosynthesis, phenolic metabolism,
67 carotenoid biosynthesis, and antioxidant defense (Booij-James et al., 2000; Xie et al., 2012).

68 Therefore, the effects of preharvest UV-C treatment on a set of quality parameters
69 including microorganism occurrence and fruit decay, photosynthetic efficiency, dry matter
70 partitioning, yield, phytochemical accumulation, and relative transcript accumulation of genes
71 putatively associated with these metabolic pathways in strawberry were monitored.

72

73 **2. Material and methods**

74 2.1 Plant material and sampling procedure

75 The experiment was conducted in two greenhouses (8 x 12 m) oriented in a north-
76 south direction and covered with low-density polyethylene film (200 µm). Eight hundred
77 seedlings of strawberry cultivar Camarosa were grown according to a crop system described
78 by Portela et al. (2012). Four hundred seedlings were designated for control without UV-C
79 application and the other four hundred for UV-C treatments. This cultivar was chosen due to
80 its vigorous growth habit. The spacing used was 30 cm between plants and 40 cm between
81 rows. All plants were fertilized following guidelines described by Sonneveld and Straver
82 (1999) with electrical conductivity (EC) adjusted to 1.5 dSm^{-1}. When a variation greater than
83 10% of the EC was observed, nutrient or water was added, while pH was maintained between
84 5.5 and 6.5. During the 45 d after transplantation (from May 7th to June 22nd) all flowers were
85 removed until plants had between ten and twelve leaves. Thereafter, typical cultural practices
86 were followed, and upon development of flower buds (starting July 22nd) two Jataí
87 (*Tetragonisca angustula*) bees' boxes were installed for pollination.

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88 Fruit were harvested during the highest productivity period, which corresponded to the 89 45th and 85th day after treatments were initiated. Each day, thirty fruit from each treatment 90 were harvested and divided into groups of 10 fruit, each group constituting a replicate. PAL 91 enzyme activity and physicochemical characterization were determined from fruit kept at - 92 80ºC. Total mesophilic bacteria and incidence of fungal decay were determined in fruit 93 harvested at 56 d after treatments were initiated. The fungal inocula present in the greenhouse 94 air was quantified during the production cycle (8, 32, 56, and 80 d after treatments were 95 initiated). Real time PCR (qPCR) analyses were carried out from leaves and fruit harvested at 96 0, 8, 32, 56, and 80 d after treatments. At the end of the crop cycle, five plants from each 97 replicate were harvested and fruit, roots, stolons, and leaves were separated to obtain dry 98 matter partitioning. Experiment timeline, showing crop cycle, UV-C treatment, and sampling 99 dates for analysis is presented in Figure 1.

100

101 2.2 UV-C treatment

102 The radiation source consisted of four germicidal bulbs (Phillips® TUV 30 103 watts/G30T8) emitting light at 254 nm. Plants were placed one meter away from the bulbs. 104 Irradiation was applied from flowering until the last harvest day (July 22nd to November 15th). 105 Each irradiation application lasted 2 min and plants received 0.5 kJ m^{-2} (UV light meter, 106 Model 232-RS-203 MRUR, Instrutherm) at 7 PM every four days, totaling 28 applications 107 (Fig. 1). UV-C dose and application intervals were established from exploratory tests using 0 108 kJ m^{-2} to 1.5 kJ m^{-2}. Just prior to each UV-C application, bees' boxes were closed and 109 removed from the greenhouses. Control plants did not receive UV-C application.

110

111 2.3 Leaf gas exchange and chlorophyll fluorescence analysis

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112 CO_2 assimilation rate (*A*; µmolm^{2}s^{-1}), stomatal conductance (*gs*; nmolm^{2}s^{-1}), and
113 intracellular CO_2 concentration (*Ci*; µmolmol air^{-1}) of leaves were monitored with a portable
114 gas exchange system infrared gas analyzer (IRGA, Heinz Walz GmbH, GFS 3000 model).
115 Measurements were performed after the beginning of UV-C treatment (July 22nd) following
116 the procedure described by Kadir and Sidhu (2006). Chlorophyll fluorescence rate (*Fv/Fm)*
117 was measured using the same equipment (Hüther et al., 2013). Evaluation of chlorophyll
118 fluorescence rate was carried out at eight-day intervals (between 9:30 and 11:00 PM), starting
119 two days before the first UV-C treatment (Fig. 1).
120

121 2.4 Dry matter partitioning, fruit yield, and physicochemical characterization

122 At the end of the crop cycle, five plants from each replicate were collected and fruit,
123 roots, stolons, and leaves were separated to obtain dry matter partitioning after drying at 70ºC
124 for 3 d . Soluble solids (SS) content was determined by refractometry and expressed as °Brix.
125 Total acidity (TA) was determined by titration and expressed as mg citric acid per kg^{-1} of
126 fresh fruit. Fruit color was measured using a colorimeter as described by Severo et al.
127 (2015a). Firmness was evaluated as described by Severo et al. (2015b).
128

129 2.5 Microorganism occurrence

130 In order to evaluate the fungal inocula present in the air of the greenhouse a passive
131 sampling was carried out. Petri plates 9 cm in diameter (0.006359 m^2 area) containing
132 Sabouraud agar, chloramphenicol, and gentamicin (BioRad63774) were used. In each
133 greenhouse, ten open plates were placed among the plants for 1 h at four intervals throughout
134 the production cycle (8, 32, 56, and 80 d after treatments were initiated). Plates were
135 incubated for 48 h at 25°C, and results were expressed as colony forming units (CFU) m^{2}h^{-1}.
136 For total mesophilic count, twenty-five grams of fruit were sampled and added to 100 mL of

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137 sterile peptone water, and a one mL aliquot was inoculated in total plate count agar (PCA)
138 (Sigma-Aldrich 70152). Plates were incubated at 35°C for 48 h and the results were expressed
139 as CFU g^{-1}. To evaluate the incidence of fungal decay, strawberries were stored in plastic
140 boxes and kept at room temperature (RT, 23 ± 2°C) and a relative humidity (RH, 85 ± 5%) for
141 3 d after harvest. Results were expressed in percentage (%) of decayed fruit. In order to assess
142 possible induction of disease resistance, a *Botrytis cinerea* strain was isolated from diseased
143 strawberry fruit and cultured on potato dextrose agar (PDA) (Sigma Aldrich 70139). As soon
144 as mycelial growth was evident, an agar plug was sub cultured on PDA until spore production
145 occurred. After 7 d the Petri dish was flooded with sterile water containing 0.02% (v/v)
146 Tween 20, filtered and diluted to a concentration of 10^4 spores per mL. After harvest, a
147 portion of the fruit was disinfected (NaClO, 100 µg L^{-1}, pH 5.0) for 2 min. Strawberries were
148 wounded (2 mm) with a sterile probe, one wound per fruit, in the equatorial zone and 20 µL
149 of a suspension containing 10^4 *Botrytis cinerea* spores per mL water were inoculated. After
150 inoculation, fruits were stored at RT for 3 d and results were expressed in % of decayed fruit.
151 This method was adapted from Pombo et al. (2011).
152

153 2.6 Phenylalanine ammonia lyase activity (PAL; EC 4.3.1.24)

154 PAL enzyme activity was determined by homogenizing fifteen grams of fresh tissue in
155 15 mL of buffer containing: 20 mM β-mercaptoethanol (Sigma Aldrich M3148), 0.1 M
156 sodium borate buffer with pH 8.8, and 5% (m/v) of polyvinylpyrrolidone (PVP) (Sigma
157 Aldrich PVP40). After filtration, the homogenate was centrifuged at 12.000 *x* g for 20 min.
158 Enzyme activity was measured by adding 1 mL of the crude enzyme preparation to a reaction
159 medium containing 1 mL of 0.2 M sodium borate buffer with pH 8.8, and 1 mL of 0.1 M L-
160 phenylalanine. After incubation for 1 h at 30ºC, the reaction was stopped by adding 0.1 mL of
161 6 N HCl and the absorbance was determined at 290 nm at intervals of 20 min for at least one

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162 hour after the addition of phenylalanine. Enzyme activity was calculated using the molar
163 extinction coefficient of $10^4 mM^{-1}cm^{-1}$ and expressed in mmol of cinnamic acid $min^{-1}g^{-1}$
164 (Zucker, 1965).

165

166 2.7 Phytochemical content and antioxidant potential

167 Total phenolic content was determined using the Folin-Ciocalteau reagent (Sigma
168 Aldrich F9252). Total anthocyanin content was determined by extraction using ethanol (pH 1)
169 and antioxidant potential was determined using the ABTS radical scavenging assay. Total
170 phenolic, total anthocyanin, and antioxidant potential analyses were performed as described
171 by Severo et al. (2015b). L-ascorbic acid content was determined spectrophotometrically
172 following Stevens et al. (2006). Folate content was determined by HPLC-UV based on a
173 method described by Delchier et al. (2012). Results were expressed on a fruit fresh weight
174 basis (ffw).

175

176 2.8 RNA extraction, cDNA synthesis, and qPCR

177 Total RNA extraction, RNA quality evaluation, reverse transcription, and qPCR were
178 performed following the protocols used by Severo et al. (2015b). Six genes were chosen
179 based on putative roles in strawberry photosynthesis, defense responses, and phytochemical
180 content: photosynthesis - light harvesting complex (*LhcIIb-1*) (Xu et al., 2012), defense
181 responses - β-1,3-glucanase (*β-1,3-Gluc*) and pathogenesis-related protein 1 (*PR-1*) (Pombo et
182 al., 2011) and phytochemical content - phenylalanine ammonia lyase (*PAL*) (Galli et al.,
183 2014), anthocyanin synthase (*ANS*) (Severo et al., 2015b), and β-galactosidase (*β-Gal*)
184 (Severo et al., 2015a, 2015b). The histone H4 (*HIDTH4*) was used as an internal standard due
185 to its expression stability under the experimental conditions (Galli et al., 2014). Leaves and

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186 fruit collected from control strawberries plants were used as baseline expression to establish
187 the relative transcript accumulation.
188
189 2.9 Experimental design and statistical analysis
190 The experiment was carried out in a completely random design with three replicates
191 using control plants without UV-C application (greenhouse 1) and plants treated with UV-C
192 (greenhouse 2). Data were analyzed for normality using a Shapiro-Wilk test, for
193 homoscedasticity using a Hartley test, and an analysis of variance (ANOVA) was conducted
194 ($\alpha = 0.05$). A post-hoc analysis was performed using a t-test ($\alpha = 0.05$). Percent data was
195 normalized before statistical analysis.
196

197 **3. Results**

198 3.1 Photosynthetic efficiency, dry matter partitioning, yield, and basic composition
199 The application of UV-C radiation (0.5 kJ m^{-2}) during cultivation resulted in the
200 reduction of CO_2 assimilation (*A*), stomatal conductance (*gs*), and intracellular CO_2
201 concentration (C*i*) of strawberries leaves on average 44%, 27%, and 49%, respectively (Figs.
202 2A, B, C). A significant reduction was also observed for chlorophyll fluorescence rate
203 (*Fv*/*Fm*) (Figs. 2D, E), indicating a possible effect of UV-C on photosystem II. UV-C
204 radiation during cultivation reduced leaf biomass by 28% and fruit yield by 20%. Root,
205 stolon, and fruit dry matter content were not affected (Figs. 2F, G, H). Although UV-C treated
206 fruit showed lower °Hue (control 32.3 °Hue, UV-C 30.2 °Hue), acidity (control 8.0, UV-C 7.5
207 in citric acid equivalent g 100^{-1} g ffw) and flesh firmness (control 3.45 N, UV-C 3.48 N) were
208 not affected.
209

210 3.2 UV-C effect on microorganisms

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211 UV-C treatment lowered fungal inocula in the air when compared to control samples
212 (Fig. 3A). Mesophilic microorganism count on the surface of strawberries was lower in fruit
213 treated with UV-C (600 CFU.g^{-1}) than in control fruit (1670 CFU.g^{-1}) (Fig. 3B). The
214 occurrence of spontaneous decay on strawberries maintained at room temperature for 3 d was
215 lower in UV-C treated fruit (39%) than control strawberry (76%) (Fig. 3C). However, when
216 fruit were inoculated with *Botrytis cinerea* spores, high levels of decay were detected for both
217 treatments (86% and 87% for UV-C and control, respectively), after three days at RT (Fig.
218 3D).
219
220 3.3 Phytochemical content
221 PAL enzyme activity increased by 18% in fruit treated with UV-C (Fig. 4A). Total
222 phenolic, total anthocyanin, L-ascorbic acid content, and antioxidant potential (Figs. 4B, C,
223 D, E, F) were higher in UV-C treated fruit (43%, 22%, 9%, 39%, respectively), while total
224 folate content was reduced (11%).
225
226 3.4 Relative transcript accumulation
227 The expression profile of control and UV-C treated plants was similar in leaf and fruit
228 tissues (Fig. 5). Photosynthesis-associated gene *LhcIIb-1* encoding for a light-harvesting
229 complex was down-regulated by UV-C while β-1,3-glucanase (*β-1,3-Gluc*), pathogenesis-
230 related protein 1 (*PR-1*), and phenylalanine ammonia lyase (*PAL*) were up-regulated by UV-
231 C. Anthocyanin synthase (*ANS*) and β-galactose dehydrogenase (*β-Gal*) gene expression
232 showed no clear pattern.
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236 **4. Discussion**

237 Postharvest UV-C radiation application increases fruit shelf life, affects phytochemical
238 content, and interferes with ripening, maturation, and senescence processes (Baka et al., 1999;
239 Charles et al., 2008a, 2008b, 2008c; González-Aguilar et al., 2007; Maharaj et al., 1999;
240 Pombo et al., 2011; Severo et al., 2015a, 2015b). Few studies have investigated the effects of
241 UV-C radiation application during cultivation (Obande et al., 2011; Xie et al., 2015). In this
242 study, photosynthetic efficiency, dry matter partitioning, fruit yield and decay, phytochemical
243 content, and relative transcript accumulation of genes putatively associated with
244 photosynthesis, defense responses, and phytochemical biosynthesis were monitored in
245 strawberries plants treated with UV-C radiation during cultivation. UV-C radiation had a
246 negative effect on leaf photosynthetic efficiency, reducing CO_2 assimilation rate (*A*), stomatal
247 opening (*gs*), and intercellular CO_2 concentration (*Ci*) (Figs. 2A, B, C). A fluorescence
248 parameter F_o measurement was taken when all photosystem reaction centers were opened
249 (plants and leaves in the dark) and a fluorescence parameter F_m measurement was taken when
250 all reaction centers were closed (maximum light) (Gurunani et al., 2015; Hürther et al., 2013;
251 Zivcak et al., 2014). High *Fv/Fm* values indicate high photosynthetic efficiency, and therefore
252 an increase in dry matter content is expected (Goltsev et al., 2009; Gurunani et al., 2015;
253 Zivcak et al., 2014). However, strawberry plants treated with UV-C showed a decrease in
254 $FV=Fm-F_o$ and *Fv/Fm* parameters, as well as a decrease in leaf dry matter content (Figs. 2D,
255 E, F). Concurrently, gene transcript accumulation of *LhcIIb-1* decreased in leaves and fruit of
256 UV-C treated plants, confirming the impact of this abiotic stress on photosynthetic
257 parameters. Topcu et al. (2015) observed that UV radiation (280–315 nm) during broccoli
258 growth promoted a decrease in total carotenoid, chlorophyll a, and chlorophyll b contents, but
259 an increase in ascorbic acid, total phenolic, and flavonoid contents.

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260 Photosynthesis is a multi-step process with successive redox reactions in which
261 photosystem II – light-harvesting complex (PSII – LhcII) is responsible for the absorption of
262 light energy (photons) by chlorophyll molecules (Gurunani et al., 2015). Under abiotic stress
263 conditions, reactive oxygen species (ROS) generated in chloroplasts lead to photoinhibition of
264 PSII–LhcII (Chen et al., 2012). According to Tikkanen et al. (2014), when light energy
265 absorbed by the PSII-LhcII pigments is higher than the energy consumed severe damage to
266 PSII may occur. Therefore, a down-regulation of *LhcIIb-1* in plants treated with UV-C may
267 have been a plant defense strategy against possible damage to the photosynthetic machinery.
268 In addition, root, stolon, and fruit dry matter contents were not affected by preharvest UV-C
269 treatment (Fig. 2F) despite the reduction in fruit yield (20%) (Figs. 2G, H).

270 Strawberry is highly susceptible to gray mold disease caused by *Botrytis cinerea* (Neri
271 et al., 2014). Fruit from strawberry plants treated with UV-C during cultivation showed lower
272 incidence of fungal decay (39%) when compared to untreated strawberries (76%). In order to
273 further understand the cause of the decreased decay promoted by UV-C application, the
274 inocula present in the air of the greenhouses and the microbial count on fruit surface were
275 monitored. In addition, strawberry fruit was also inoculated with *Botrytis cinerea* spores. UV-
276 C radiation promoted a disinfectant action in both the greenhouse environment and the fruit
277 surface (Figs. 3A, B, C), and increased transcript accumulation of defense response genes *β-*
278 *1,3-Gluc* and *PR-1*. These events combined likely contributed to the lower occurrence of
279 fungal decay in strawberry treated with UV-C radiation before inoculation with *Botrytis*
280 *cinerea* spores. However, it is known that gene expression does not always lead to
281 physiological responses, since many post-transcriptional and post-translational events may
282 occur which interfere with the outcome (Mazzucotelli et a., 2008). In addition, strawberry
283 resistance to a variety of pathogens has been reported to be mostly polygenic and
284 quantitatively inherited (Lewers et al., 2003). In general, a plant defense system is composed

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285 of cell wall structural components, phytochemicals, and PR-proteins (Amil-Ruiz et al., 2011).
286 Thus it becomes difficult to attribute an inhibition of fungal decay only to an increase of *β-*
287 *1,3-Gluc* and *PR-1* transcripts, since all components of the plant defense system may
288 synergistically be playing a role in inhibition of fungal decay (Amil-Ruiz et al., 2011).
289 Moreover, a reduction in spore and bacterial count upon UV-C radiation was evident.

290 In the present study, inoculation of fruit with *Botrytis cinerea* spores led to high
291 disease symptom development in both control and UV-C treated fruit (85%) (Fig. 3D). This
292 result differed from previous reports that showed a reduction of fruit decay by UV-C radiation
293 after inoculation with *Botrytis cinerea* spores (Pombo et al. 2011; Charles et al. 2008a, 2008b,
294 2008c). However, the treatment used in the previously mentioned studies was a strong single
295 dose of UV-C, applied to fruit postharvest. In the present study, weaker doses of UV-C
296 radiation were applied from flowering to harvest, constituting a different stress condition. In
297 addition, *Botrytis cinerea* spore inoculation by wounding of the fruit surface may represent an
298 extreme situation, whereby even the strongest defense system may not be able to counteract.

299 The relationship between plant and pathogen, and an induction of the plant defense
300 system by biotic and abiotic stresses appear to be quite complex and are not fully understood
301 (Amil-Ruiz et al., 2011). Several authors have observed that cell wall thickness and softening
302 are correlated with pathogen resistance (Cantu et al., 2008; Guidarelli et al., 2011).
303 Furthermore, the effect of postharvest UV-C radiation on fruit cell wall modification and flesh
304 firmness has also been shown (Baka et al., 1999; Maharaj et al., 1999; Charles et al., 2008b,
305 2008c). In this study, no difference in flesh firmness or fruit decay incidence after inoculation
306 with *Botrytis cinerea* spores were observed between control and UV-C treated strawberries.

307 After pathogen inoculation, signaling and metabolic changes due to cell wall injury
308 and pathogen perception may occur (Amil-Ruiz et al., 2011; Neri et al., 2014). Depending on
309 fruit ripening stage, innate immunity, pre-formed mechanical barriers, and a response of

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310 resistance induction, the fruit would be able to counteract the disease (Amil-Ruiz et al., 2011).
311 However, Neri et al., (2014) showed that after inoculation, the physical injury of tissues
312 creates significant changes in strawberry volatiles emission that stimulated *Botrytis cinerea*
313 growth compared to intact fruit. In the present study, strawberry was submitted to a stress
314 condition from flowering to harvest, in addition to inoculation by wounding the fruit surface,
315 which likely accelerated fruit metabolism resulting in high incidence of gray mold disease.

316 On the other hand, UV-C treatment during cultivation promoted antioxidant
317 metabolism (Fig. 4). Plants exposed to abiotic stress conditions have increased ROS content,
318 which in turn can cause photoinhibition of the photosynthesis photosystem II repair process
319 (Gurunani et al., 2015; Lemoine et al., 2010). To cope with this stress condition, plants
320 synthesize ROS-scavenging enzymes and antioxidants, such as α-tocopherol, L-ascorbic acid,
321 carotenoids, and phenolic compounds that can reduce the rate of photoinhibition (Gill and
322 Tuteja, 2010; Gurunani et al., 2015). In this study however, an increase in phytochemical
323 content was accompanied by a decrease in yield, probably due to the stress condition
324 generated by UV-C application from flowering to harvest. Folate content was also lower in
325 UV-C treated fruit. Since many phenolic compounds and folate are derived from the
326 shikimate pathway with common intermediates such as chorismate, it is plausible that UV-C
327 directed one pathway instead of another (Bekaert et al., 2008).

328 Preharvest application of UV-C radiation on strawberries from flowering to harvest
329 increased phenylalanine ammonia lyase activity, phenolic compounds, including
330 anthocyanins, L-ascorbic acid, and antioxidant potential. However, decreased photosynthetic
331 efficiency and a 20% yield reduction per plant, which corresponded on average to 223 g of
332 fruit, were observed. Considering the mass balance of fruit yield and phenolic concentration,
333 phenolic content was more than 20% higher in treated fruit, which compensated for the yield

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334 reduction. Furthermore, UV-C radiation applied during strawberry cultivation decreased
335 greenhouse spore count and spontaneous development of *Botrytis cinerea* in fruit postharvest.
336

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342 **5. References**

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500 **Fig. 1.** Experiment timeline with crop cycle (days after transplanting) and sampling times (▲)
501 – UV-C applications, (●) – photosynthetic measurements, (◆) – physicochemical and enzyme
502 activity determinations (highest productivity period), (⬆) – microorganism occurrence, (■) –
503 qPCR and dates for determination of fungal inocula in the air, and (✹) – dry matter
504 partitioning determination.
505
506 **Fig. 2.** Effect of preharvest UV-C treatment on CO_2 assimilation rate (A), stomatal
507 conductance (B), intracellular CO_2 (C), fluorescence (D), quantum yield efficiency of
508 photosystem II (*Fv/Fm*) (E), dry matter partitioning (F), fruit yield per plant (G) and total
509 yield (H) in control (—●—; ▬) and UV-C treated fruit (···○···;▭). Asterisks indicate
510 level of significance at P≤0.05. Vertical bars indicate standard deviation.
511
512 **Fig. 3.** Occurrence of fungi in the air (A), number of mesophilic microorganisms (B),
513 incidence of fungal decay without inoculation with *Botrytis cinerea* spores (C), incidence of
514 fungal decay with inoculation of 10^4 *Botrytis cinerea* spores (D) in Control strawberry (—●—
515 ; ▬) and UV-C treated fruit (···○···;▭). Asterisks indicate level of significance at P≤0.05.
516 Vertical bars indicate standard deviation.
517
518 **Fig. 4.** Phenylalanine ammonia lyase (PAL) activity (A), total phenolic content (B), total
519 anthocyanin content (C), ascorbic acid content (D), antioxidant activity (E) and folate content
520 (F) in Control strawberry (▬) and UV-C treated fruit (▭). Asterisks indicate level of
521 significance at P≤0.05. Vertical bars indicate standard deviation.
522
523 **Fig. 5.** Relative transcript accumulation of genes encoding enzymes associated with
524 photosynthesis, resistance to pathogens, phenolic compounds biosynthesis and L-ascorbic

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525 acid biosynthesis in leaves of control strawberries and UV-C treated fruit. Samples were
526 collected at 0, 8, 32, 56, and 80 d after treatment. Leaves and fruit collected from control
527 strawberries plants were used as baseline expression to establish the relative transcript
528 accumulation. Values were normalized by applying log2. Transcript accumulation is
529 represented in Multi Experiment Viewer software (TIGR MeV). Green color on the left
530 represents the minimum expression level, black color in the middle represents the median
531 level and red color represents the maximum transcription level observed.

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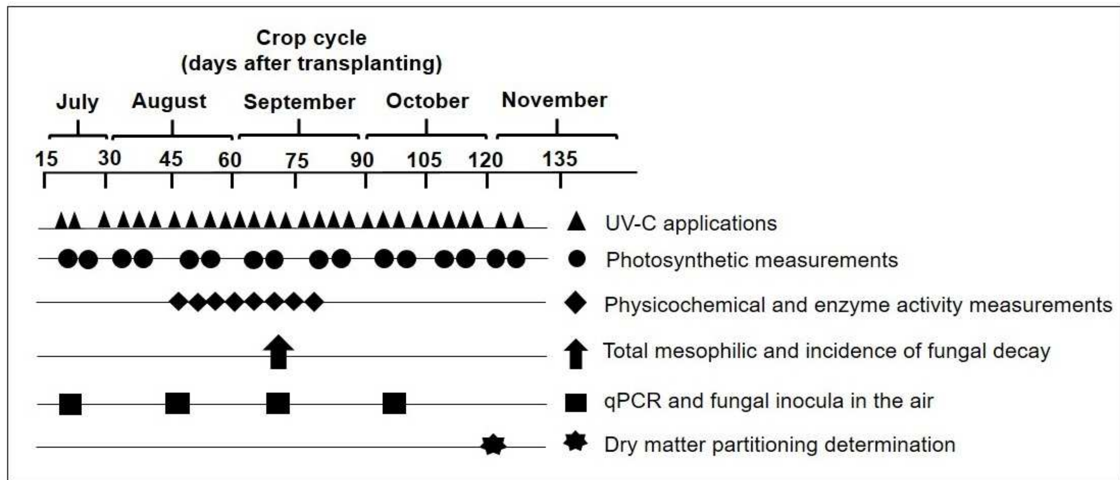

Fig. 1. Experiment timeline with crop cycle (days after transplanting) and sampling times (▲) – UV-C applications, (●) – photosynthetic measurements, (◆) – physicochemical and enzyme activity determinations (highest productivity period), (🠉) – microorganism occurrence, (■) – qPCR and dates for determination of fungal inocula in the air, and (✸) – dry matter partitioning determination.

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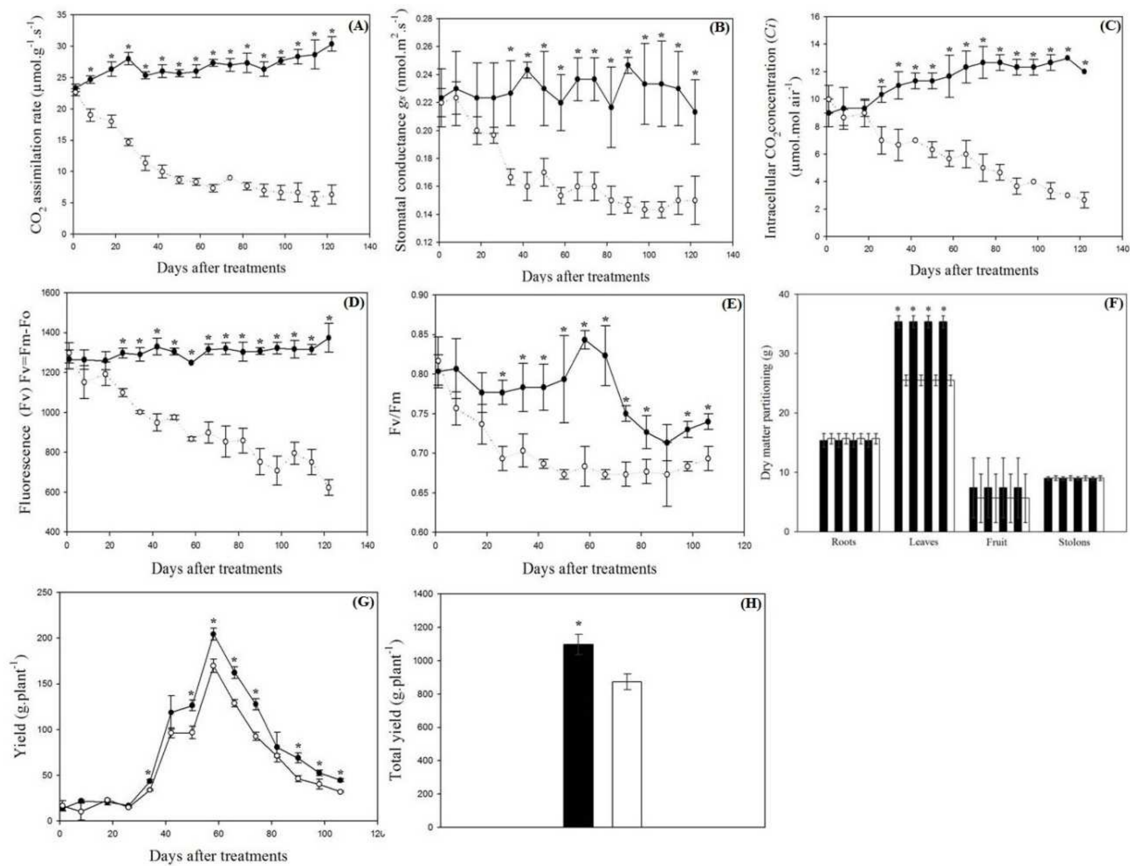

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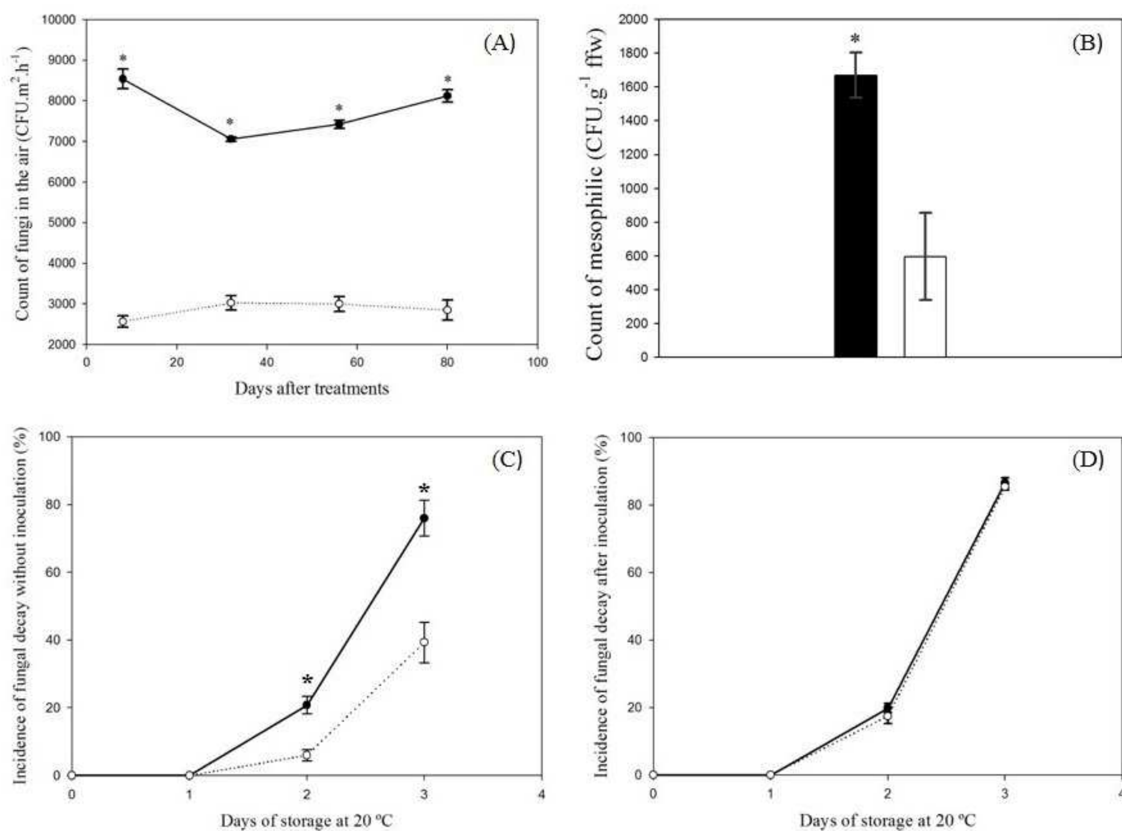

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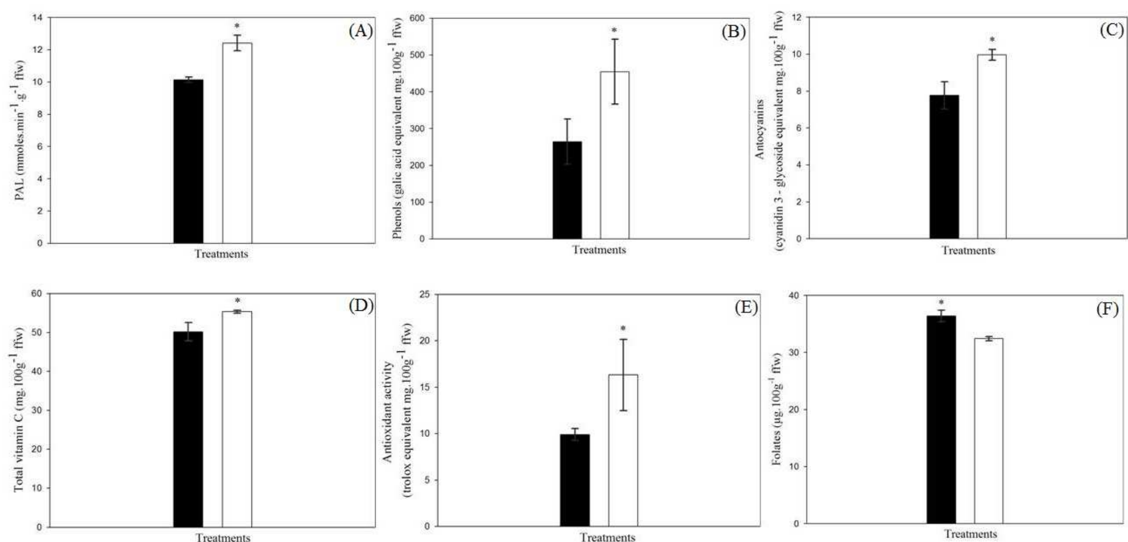

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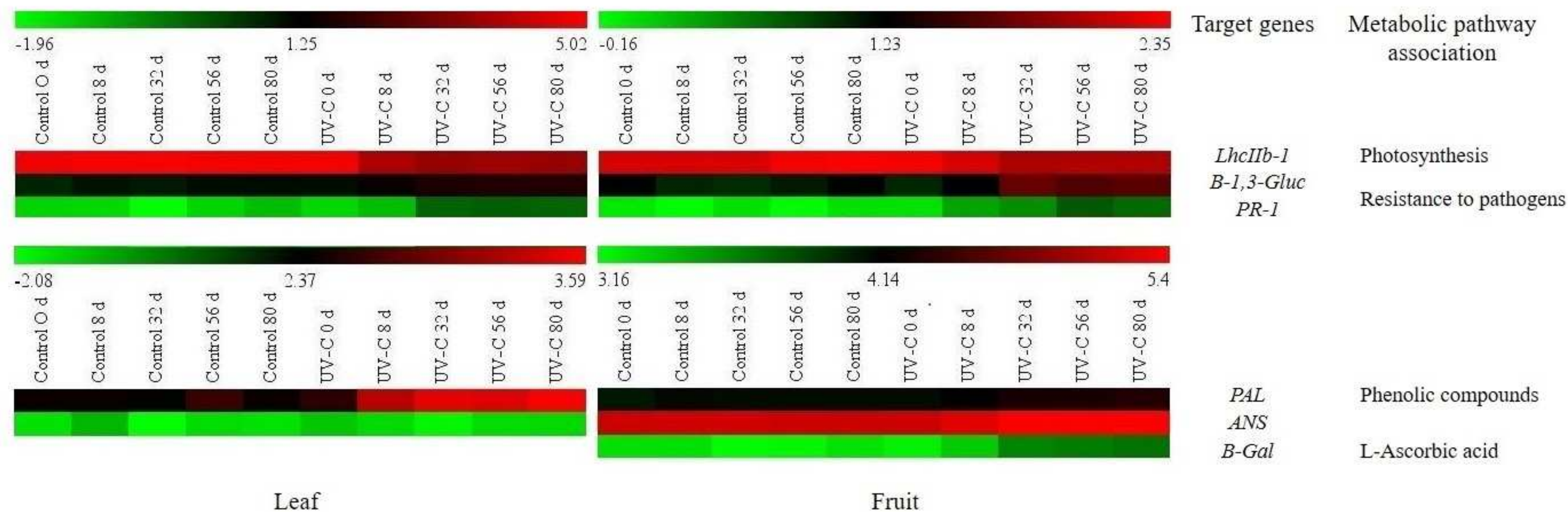

Fig. 5. Relative transcript accumulation of genes encoding enzymes associated with photosynthesis, resistance to pathogens, phenolic compounds biosynthesis and L-ascorbic acid biosynthesis in leaves of control strawberries and UV-C treated fruit. Samples were collected at 0, 8, 32, 56, and 80 d after treatment. Leaves and fruit collected from control strawberries plants were used as baseline expression to establish the relative transcript accumulation. Values were normalized by applying log2. Transcript accumulation is represented in Multi Experiment Viewer software (TIGR MeV). Green color on the left represents the minimum expression level, black color in the middle represents the median level and red color represents the maximum transcription level observed.

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Photosynthetic efficiency and *light harvest complex* mRNA accumulation were down regulated by UV-C

Preharvest UV-C lowered yields and reduced leaf dry matter content

Preharvest UV-C promoted antioxidant metabolism activation and prevented fruit decay

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Contribution

All authors designed research, conducted experiments and analyzed data. Cesar Valmor Rombaldi, Fabio Clasen Chaves and Catherine Renard contributed for reagents and analytical tools. All authors wrote, read and approved the manuscript.

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